

Reproductive behaviour of Odonata: the history of a mystery¹

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Abstract

The main, externally visible components of odonate reproductive behaviour were known from published accounts for about 300 years before sperm displacement during copulation was first described. The latter discovery, revealed by Jonathan Waage in 1979, revolutionised the interpretation of odonate reproductive behaviour, allowing it for the first time to be interpreted convincingly in the context of sexual selection and the evolution of mating systems. This insight has been a prerequisite for elegant, ongoing work on mechanisms of sperm displacement and sperm precedence in Odonata.

Introduction

Nowadays, as odonatologists pursue their chosen interest, some of them tend to take for granted the corpus of knowledge that they have inherited. To some extent this is understandable and inevitable: all researchers have to use existing knowledge as a departure point for future investigation. Nevertheless, it can sometimes be both instructive and humbling to trace the path of discovery by which such knowledge has been acquired. In this article I shall do this for the most remarkable and influential discovery ever made in odonatology, and one which has had a large impact on the perceptions, not only of odonatologists, but of biologists in general. I refer to the discovery of sperm displacement as a component of reproductive behaviour of Odonata. For most of the 50 or so years during which I have been associated with odonatology, sperm displacement in Odonata was unknown; so students of the order lacked the information needed to place odonate reproductive behaviour in a satisfying evolutionary context.

All odonatologists are familiar with the sequence of events that characterises reproductive behaviour of dragonflies. The most obvious behaviour that sets Odonata apart from other insects is the singular placement of the male genitalia – on the ventral surface of abdominal segments 2 and 3. This correlates with the unique copulatory posture, the so-called ‘copulation wheel’, the means by which insemination is accomplished.

¹ This article is based on an oral presentation to the Regional Meeting of the Worldwide Dragonfly Association held in Leiden, The Netherlands in June 2002. I dedicate it, with gratitude and respect, to that giant among Dutch biologists, Jan Swammerdam (1637-1680) who graduated as Doctor of Medicine in Leiden in 1667, just before he devoted his remarkable talents entirely to the study of insects.

Copulation posture

Reflecting on the long history of odonatology (see Corbet 1991), one must accept the possibility that some perceptive observers saw and understood the main elements of reproductive behaviour in Odonata earlier than the published record reveals, but this supposition can only be speculative: the development of knowledge can be traced only from published accounts, and these show that little or nothing was understood about odonate reproductive behaviour up to the early 17th Century (see Moufet 1634). Indeed, all that Thomas Moufet (1553-1604) had to say about reproductive behaviour of dragonflies – “*Libellulae maximae*” in his terminology – was that “all of them have forked tails and with these they couple, remaining long in the act of generation” (Moufet 1634: 939). However, in the 1670s (but published later), Jan Swammerdam (1637-1680) correctly described and illustrated the tandem link, the copulation wheel (Fig. 1) and the position of the male secondary genitalia (Swammerdam 1737, 1738, 1758). During the next Century the peerless René-Antoine Ferchault de Réaumur (1683-1757) (“a modern Leonardo”, Cole 1949: 484), gave a detailed and accurate account of odonate reproductive behaviour, including endophytic oviposition (Réaumur 1742: 452). At about the same time the distinguished North American naturalist, John Bartram (1699-1777) of Pennsylvania, communicated his observations of dragonfly behaviour to European scientists, who made his work known through periodicals of learned societies (e.g. Collinson 1750). Bartram correctly described adoption of the tandem link, formation of the wheel position, impregnation, and exophytic oviposition in the hovering mode. In 1845 the English naturalist William Frederick Evans described the copulation wheel but dismissed the notion that it is a copulatory position, quoting Carl Hermann Burmeister who had averred (1836: 218) that actually “the males fly at sitting females and rapidly copulate with them, like the flies”, and saying that other observers had confirmed this observation. Burmeister (1836: 218) had further stated (somewhat quaintly to contemporary perceptions) that what we now know as the copulation wheel “is merely an expression of mutual inclination” However in 1890 another English naturalist, W. Harcourt Bath (Anonymous 1889), correctly described and interpreted the tandem and copulatory positions and the two main modes of oviposition, as did his contemporary and compatriot William John Lucas (1900). In his catalogue of the Odonata near Philadelphia – a milestone among accounts of odonate biology – Philip P. Calvert (1893: 184-186) described the secondary genitalia and primary genital pore of the male and also (p. 188) intramale sperm translocation (as occurring usually, but not invariably, *before* formation of the tandem link) and mentioned that insemination results from sperm residing in the receptaculum seminis and the bursa copulatrix, reporting further that eggs are fertilized as they pass down the vagina during the process of oviposition. In this remarkable account Calvert (pp. 189-190) described the modes of oviposition and noted that most individuals probably mate more than once. He observed that females can mate even during oviposition. Seen in historical context, these observations by Calvert represent a major contribution to our understanding of odonate reproductive behaviour, unequalled or significantly extended for the next 80 years. In the next major synoptic account of odonate biology, Carl Wesenberg-Lund (1913) of Denmark gave a correct and informed interpretation of reproductive behaviour and the arrangement of the structures involved, commenting that

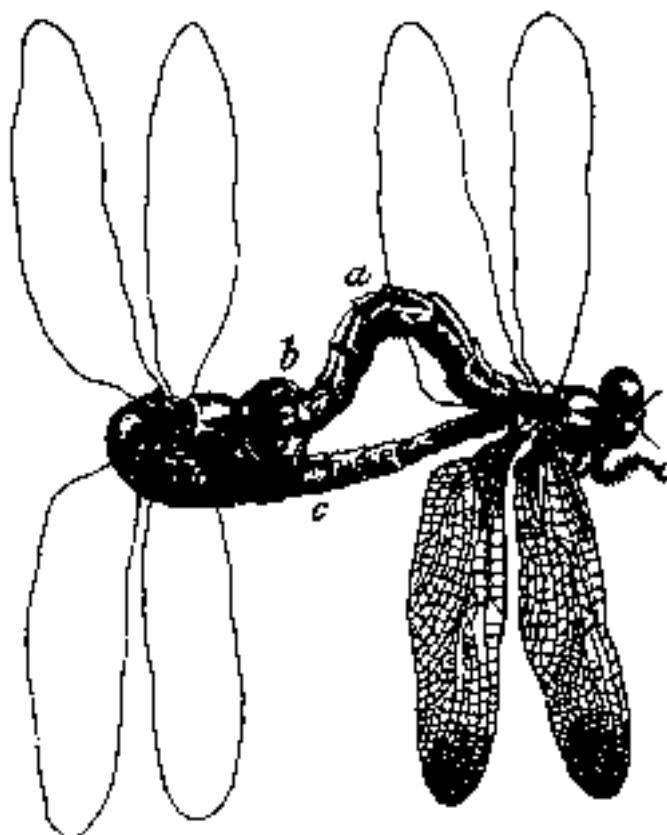


Figure 1. Probably the first correct illustration of the copulation wheel. From Swammerdam (executed before 1669, published 1758: plate 12, fig. 3). Swammerdam's designations: "Fig. III, Of the copulation of the Dragon-flies. a, The tail of the male; b, The female receiving into her neck the tail of the male, and embracing it with her legs; c, The tail of the female turned toward the breast of the male."

the mode of copulation is well suited for insects such as Odonata that are active fliers. Like Edward Bruce Williamson (1906) before him, Wesenborg-Lund noted that intra-male sperm translocation usually occurs promptly *after* tandem formation, a view that is now widely held.

In the next major odonatological work, "The biology of dragonflies", Robin John Tillyard (1917) described the morphology of the reproductive organs in detail but curiously said almost nothing about reproductive behaviour, confining such remarks to a description of courtship. This omission is surprising, bearing in mind the distinguished contributions of Tillyard's predecessors and the great breadth of his own odonatological knowledge. Describing the morphology of the zygoteran penis, Tillyard (1917: 217) remarked "It is difficult to say what part a poorly developed organ of this kind can play

in copulation, unless it serves as a kind of hinge or link, by means of which the female pore is held in contact with the [penis] vesicle."

Territorial behaviour

Beginning with Williamson's report in 1899 that *Celithemis* males exhibited proprietary defence of a particular area over water, followed by his observation (1923) that such defence by *Erythemis* males protected conspecific females against interference while ovipositing, the recognition slowly grew up to the early 1950s that male dragonflies exhibited a form of territoriality (see review by Jacobs 1955). The persistence with which a male occupied, and drove other males from, a defended space at the reproductive site had already been established by marking individual males in a classic study by Douglas St. Quentin (1934) in which the author attributed such behaviour, not to the pre-empting of visiting females, but to the defence of a foraging area, or "Jagdrevier." Though St. Quentin overlooked the main significance of territorial defence, his was a seminal paper, and it stimulated important work in the 1950s, notably by Norman Moore (1952, 1957), Merle Jacobs (1955), Gerald Mayer (1957), Edmund Kormondy (1959), and Rudolf Zahner (1959), and in the 1960s by George & Juanda Bick (1961), Clifford Johnson (1962), and Ilmari Pajunen (1962), contributions that were reviewed by St. Quentin (1964) and Corbet (1962), who cited additional studies by Shozo Ishida (1958) and Akira Taketo (1958).

The sexual significance of odonate 'territorial' behaviour, though inferred by Moore in 1952, was first demonstrated unequivocally by Jacobs (1955) for *Plathemis lydia* (Drury) and *Perithemis tenera* (Say), and reported by him in a milestone publication that was to establish beyond doubt the reproductive significance of territorial behaviour and thereby provide a sound theoretical basis for subsequent studies that investigated it from a sexual perspective (reviews by Kormondy 1961; Bick 1972; Parr 1983; Kaiser 1984; Corbet 1999).

Taking stock in 1962

Despite these significant advances and the obviously close analogies with territoriality in birds, a satisfying evolutionary rationalization of dragonfly reproductive behaviour remained elusive. For example, in my 1962 book I summarized (Corbet 1962: 181-182) what I then perceived as the various ways that behaviour patterns met the ecological requirements faced by reproducing dragonflies:

- **Meeting of the sexes** is accomplished by both sexes exercising the same habitat selection to meet at the rendezvous.
- **Sexual isolation** is achieved by, *inter alia*, accurate spatial and temporal coincidence, visual recognition and physical incompatibility.
- **Disturbance of copulation** is mitigated by males being localised and spaced out as a result of their aggressive behaviour, by the duration of copulation being very brief

(sic), and by the pair then leaving the rendezvous.

- **Male interaction** selects for male maturity, potency and vigour since males deficient in these attributes are less able to resist displacement at mating sites.
- **The ovipositing female is protected against predation** by the male arriving at the rendezvous before her and testing it for safety. **She is protected against male interference** by male territorial behaviour, by males arriving at the rendezvous earlier than females and therefore achieving stability before females arrive, by the male guarding or remaining in tandem with the ovipositing female, by the female not being recognized by males while ovipositing or, more rarely, by oviposition occurring at a time or place other than the mating rendezvous.
- **Selection of the appropriate rendezvous by both sexes** ensures that eggs are laid in a site suitable for survival of the larvae.
- **Overpopulation of the breeding site** is mitigated by male interaction and by females being driven away when male competition is intense.

It is noteworthy that none of these behavioural adaptations identified in 1962 embodies what we now recognize as the central evolutionary significance of odonate reproductive behaviour.

Sperm competition

A development of immeasurable significance for odonatology was the prediction by Geoffrey Parker (1970) that sperm competition occurs in Odonata. It was recognized then that Odonata exhibited the four prerequisites for sperm competition to be adaptively appropriate, namely:

- Females mate more than once.
- Inseminated females store sperm in organs accessible to the male.
- The distal segment of the penis bears structures able to remove or reposition sperm.
- The male guards the female during post-copulatory oviposition.

In 1971, in his Ph.D. thesis on reproductive behaviour of *Calopteryx maculata* (Beauvois), a graduate student at the University of Michigan, Jonathan Waage, recommended topics deserving future study. Inter alia these were: the acquisition of more information on the nature of sperm translocation and insemination in *Calopteryx* and other species of Odonata and, especially, the photographic recording of events associated with sperm translocation and the engaging of the genitalia during copulation. Waage commented also that preservation of pairs in copulation and later dissection would be useful. He did not mention sperm displacement but, in view of Parker's (1970) paper, he may well have had it in mind, although Parker's paper did not find a place in Waage's bibliography.

Anyway, as every odonatologist knows, in 1979 the long-standing problem was solved with Waage's paper in 'Science' (1979). This elegant publication constituted the Rosetta Stone needed to understand the biological significance of reproductive behaviour

in Odonata, combining as it did the methods of ethology and scanning electron microscopy. After Waage's finding, everything abruptly fell into place, and the way forward was paved for the detailed studies of Peter Miller (e.g. 1991) on the functional morphology of the male and female reproductive organs, of Waage himself (1984) and, for example, of Mike Siva-Jothy (1988), Yoshitaka Tsubaki (Siva-Jothy & Tsubaki 1994), Margaret McVey (1988), Burrell Smittle (McVey & Smittle 1984), Niko Michiels (1989) and Alex Córdoba-Aguilar (1998, 2002, 2003) that have done much to clarify the different ways in which sperm precedence can be accomplished. Such work, in turn, has led to the elucidation of ways in which females can exert choice over the paternity of their eggs (reviews by Fincke et al. 1997 and Corbet 1999: 537–538). One can imagine how excited Swammerdam, certainly one of the greatest naturalists and micro-anatomists of all time, would have been to learn of the methods used by Waage to make his discovery and of the discovery itself. The work by Waage and those who have built on it also laid the ground for synoptic works on the evolution of insect mating systems in which Odonata feature prominently, such as the book by Thornhill & Alcock (1983).

It took a long time for the odonate Rosetta Stone to be discovered. Reviewing the sequence of events that led up to it, we find that the four behavioural prerequisites for sperm displacement (see above) have been well known since the morphology of the penis was first described in the late 19th Century (cf. Calvert 1893; Pfau 1971). Remarkably, there exists a paper by Elliot Pinhey (published in 1969, ten years before Waage's discovery) that makes eerie reading today, because Pinhey came extremely close to discovering sperm displacement at that time. Finding that copulating pairs of *Ischnura senegalensis* Rambur would remain firmly attached to each other after death, Pinhey cleared and mounted the linked genitalia and illustrated what he saw. What he showed (Fig. 2) was that the flagella of the penis lodge snugly *inside* the caecum of the female bursa, an arrangement that we now know enables sperm displacement to be effected. Waage knew of this paper by Pinhey and cited it in his thesis, though without commenting on its great significance. One may suppose that one reason why it was Waage, and not Pinhey, who discovered sperm displacement in Odonata is that Waage, as a young academic at Brown University, Rhode Island, would have been familiar with contemporary biological literature, unlike Pinhey, who was a full-time taxonomist at the National Museums in Bulawayo, Southern Rhodesia. From my own experience of working in relative isolation in Africa, I think it unlikely that Pinhey would have had regular access to the journal 'Biological Reviews' in which Parker's 1970 paper was published.

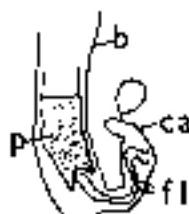


Figure 2. *Ischnura senegalensis*. The flagella (fl) of the penis (p) lodged inside the caecum (ca) of the female bursa (b) during copulation. After Pinhey (1969).

Epilogue

This brief history of the elucidation of reproductive behaviour in Odonata must surely represent one of the most exciting chapters in the history of entomology; and odonatologists are privileged to have experienced it within their field. It certainly revolutionized my perception of dragonfly biology. Odonatologists, as inheritors of these discoveries made by their illustrious predecessors, are fortunate indeed. As the poet and essayist Samuel Taylor Coleridge wrote (1818): “the dwarf sees farther than the giant, when he has the giant’s shoulder to mount on.”

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